SOME EUROPEAN PROVIVERRINI
(MAMMALIA, DELTATHERIDIA)

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ABSTRACT. A generic revision of the Proviverrini is made, with special attention to European material from the middle Eocene. Phylogeny and parallel evolution are discussed. *Proviverra* is made identifiable; *Sinopa, Geiselotherium, Leonhardtina,* and *Prorhyzaena* are synonymized with it. Specimens of the Miacidae and Oxyaenidae, and one of unknown affinities, are described from the Eocene of Europe. New taxa are the following: Deltatheridia, new order; *Arfia,* new genus; *Prototomus torvidus, Cynohyaenodon trux, Prodissopsalis phonax, P. theriodis,* and *Miacis*? *macintyri,* new species.

WHILE in Europe in 1963 I had the opportunity to examine material of a number of species of European creodonts, especially middle Eocene proviverrines. The following account, together with another paper (Van Valen, in press) and one by R. J. G. Savage (in press), provides the framework for a revision of the known Old World proviverrines. Early Eocene specimens recently collected by D. E. Russell, D. E. Savage, and P. Louis will provide further information when described. I have elsewhere (Van Valen, in press) reduced the subfamily Proviverrinae to the rank of a tribe in the Hyaenodontinae, family Hyaenodontidae, which I include in a new order, Deltatheridia. Because the publication date of that long paper is still uncertain although it was submitted for publication in the spring of 1962, I will give here a brief diagnosis of the Deltatheridia. The drawings of teeth were made on quadrille paper using a reticule in a binocular microscope unless otherwise stated. The following abbreviations are used: BM, British Museum (Natural History), Department of Palaeontology; MME, Museum für Mitteldeutsche Erdgeschichte, Halle/Saale; NMB, Naturhistorische Museum, Basel.

Order DELTATHERIDIA, nov.

Diagnosis. Insectivorous or carnivorous placental mammals usually with the following characters: tall cusps on the teeth; distinct paraconid; relatively close paracone and metacone; relatively wide stylar shelf; persistent embrasure shear on the molars, which have a prominent metastyle and no hypocone; no interradicular crests; premolars not molariform; fissured ungual phalanges; primitive placental pattern of internal carotid circulation; alisphenoid canal present.

Included groups. The order is based equally on the Palaeoryctidae (including Deltatheridiidae), Hyaenodontidae (including Limnocyonidae), and Oxyaenidae, with ordinal rank separate from the Insectivora because of the inclusion of the latter two families and separate from the Carnivora because close phyletic affinity with the Miacidae is improbable and predation clearly originated independently in the two groups. The Didy-

moconidae are also included, and the Micropternodontidae and some or all zalambdo-donts, especially the Tenrecidae (including Potamogalidae and Apternodontidae) and Chrysochloridae, may also fall here. The origin of the Oxyaenoidea from the Palaeoryc-tidae is shown by Van Valen (in press), where other phylogenetic and anatomical matters are also discussed.

GENERA AND SPECIES OF PROVIVERRINI

The following genera and species have previously been described or are described in the present paper. Taxa I regard as of uncertain validity are preceded by a question mark; type species of genera considered valid are preceded by an asterisk. Only papers giving original information or interpretations are cited.

?*Prototomus* Cope 1874, p. 13 [? = *Protoproviverra* (not *Protoviverra*) Lemoine 1891 (May), p. 272; not *Protoproviverra* Ameghino 1891 (August), which was replaced by *Amphiproviverra* Ameghino 1891, and is now included in *Thylacodictis* Mercerat, 1891], validation of name pending.

    *Prototomus viverrinus Cope 1874, p. 13. Early Eocene, Wasatchian; New Mexico and Wyoming. See also Cope (1877, pp. 109, 112), Matthew (1901, p. 27), Matthew (1909, p. 470), Matthew (1915, p. 83), McKenna (1960, p. 92), Gazin (1962, p. 54), Van Valen (in press). Validation of the name is pending.

    Prototomus multicuspis (Cope 1875, p. 10). Early Eocene, Wasatchian; New Mexico and Wyoming. See also Cope (1877, pp. 112, 116), Matthew (1901, p. 27), Matthew (1915, p. 80), Gazin (1962, p. 55).

    ?*Prototomus vulpecula* (Matthew 1915, p. 80). Early Eocene, Wasatchian; Wyoming and Colorado. See also Gazin (1952, p. 53), Robinson (1960, p. 1), Gazin (1962, p. 55).

    Prototomus mordax (Matthew 1915, p. 73). Early Eocene, Graybullian; Wyoming. See also Denison (1938, p. 241), Van Valen (in press).

    ?*Prototomus secundaria* (Cope 1875, p. 9). Early Eocene, Wasatchian; New Mexico, ?Wyoming. See also Cope (1877, p. 115), Matthew (1901, p. 27), Matthew (1915, p. 82), McKenna (1960, p. 91), Van Valen (in press).

    Prototomus palaeonictides (Lemoine 1880, p. 5) [= *Protoproviverra pomelii* Lemoine (1891, p. 265), based on the same specimen]. Early Eocene, late Ypresian; France. See also Teilhard (1921, p. 50 or 58), Louis (1963, p. 87), Van Valen (in press).

    Prototomus torvidus, new species. Middle Eocene, Lutetian; Switzerland.

Arfia, new genus.

    *Arfia opisthotoma (Matthew 1901, p. 28). Early Eocene, Graybullian; Wyoming. See also Matthew (1915, p. 73).

    ?*Arfia shoshoniensis* (Matthew 1915, p. 73). Early Eocene, Graybullian; Wyoming.

Tritemnodon Matthew (1906, p. 25).

    Tritemnodon strenua (Cope 1875, p. 10). Early Eocene, Wasatchian; New Mexico and Wyoming. See also Cope (1877, p. 117), Matthew (1901, p. 26), Matthew (1915, p. 74), Gazin (1952, p. 54), Gazin (1962, p. 56).

    Tritemnodon hians (Cope 1877, p. 118). Early Eocene, Wasatchian; New Mexico and Wyoming. See also Matthew (1901, p. 25), Matthew (1915, p. 75).

    Tritemnodon whitiae (Cope 1882, p. 161). Early Eocene, Lostcabinian; Wyoming. See also Cope (1884, p. 292), Matthew (1901, p. 26), Matthew (1906, pp. 207, 209), Matthew (1915, p. 84).

    *Tritemnodon agilis (Marsh, 1872, p. 204) [= *Stypolophus brevicalcaratus* Cope (1872b, p. 469); = *Sinopa gracilis* Wortman (1902, pp. 17, 201)]. Middle Eocene, Bridgerian; Wyoming. See also Cope (1884, p. 291), Matthew (1901, p. 24), Wortman (1902, p. 437), Matthew (1906, pp. 207, 209), Matthew (1909, p. 475), Thorpe (1923, p. 37).

Proviverra Rütimeyer 1862, p. 80 [= *Sinopa* Leidy 1871, p. 116; = *Stypolophus* Cope 1872a, p. 1;

= *Prorhyzaena* Rütimeyer 1891, p. 105; = *Leonhardtina* Matthes 1952, p. 223; = *Geiselotherium* Matthes 1952, p. 225].

Proviverra rapax (Leidy 1871, p. 116). Middle Eocene, Bridgerian; Wyoming. See also Wortman (1902, p. 435), Matthew (1906, pp. 207, 209), Matthew (1909, pp. 464, 465, 471).

?*Proviverra rapax lania* (Matthew 1909, p. 472). Middle Eocene, Bridgerian; Wyoming.

?*Proviverra grangeri* (Matthew 1906, p. 206). Middle Eocene, Bridgerian; Wyoming.

?*Proviverra pungens* (Cope 1872*a*, p. 1). Middle Eocene, Bridgerian; Wyoming. See also Cope (1884, p. 291), Matthew (1901, p. 24), Wortman (1902, p. 436), Matthew (1906, p. 209), Matthew (1909, p. 472).

?*Proviverra minor* (Wortman 1902, p. 17). Middle Eocene, Bridgerian; Wyoming. See also Matthew (1906, pp. 207, 209), Matthew (1909, p. 473), Thorpe (1923, p. 35). If this species is shown to be valid and if both it and Filhol's *Cynohyaenodon minor* prove referable to *Proviverra*, then Wortman's species must be renamed as it would be a secondary homonym. Probably at least one Bridgerian species other than *P. rapax* is valid, but which this (or these) may be is now uncertain.

?*Proviverra major* (Wortman 1902, p. 18). Middle Eocene, Bridgerian; Wyoming. See also Matthew (1906, pp. 207, 209), Matthew (1909, p. 473), Thorpe (1923, p. 36).

*Proviverra typica Rütimeyer 1862, p. 80 [= *Prorhyzaena egerkingiae* Rütimeyer, 1891, p. 105]. Middle Eocene, Lutetian; Switzerland. See also Schlosser (1887, p. 213), Rütimeyer (1891, p. 102).

Proviverra gracilis (Matthes 1952, p. 223) [= *Geiselotherium pilzi* Matthes 1952, p. 225]. Middle Eocene, Lutetian; Germany.

Proviverra minor (Filhol 1877, p. 28). Late Eocene, Ludian; France. See also Schlosser (1887, p. 216), Filhol (1888, p. 191), Martin (1906, pp. 417, 420, 421).

Cynohyaenodon Filhol 1873, p. 87 [= *Pseudosinopa* Depéret 1917, p. 172].

Cynohyaenodon trux, new species. Middle Eocene, Lutetian; Switzerland.

Cynohyaenodon ruetimeyeri (Depéret 1917, p. 172). Middle Eocene, Lutetian; Switzerland.

*Cynohyaenodon cayluxi (Filhol 1873, p. 87). Late Eocene, Ludian; ?Early Oligocene, ?Sannoisian; France. See also Filhol (1877, p. 7), Gaudry (1878, p. 20), Cope (1884, p. 289), Schlosser (1887, p. 217), Filhol (1888, p. 190), Smith (1902, p. 400), Martin (1906, pp. 420, 422), Matthew (1906, p. 209), Edinger (1929, p. 151), Russell and McKenna (1962, p. 277).

Cynohyaenodon leenhardti Martin 1906, p. 420. Late Eocene, Ludian; France.

Prodissopsalis Matthes 1952, p. 206 [= *Imperatoria* Matthes 1952, p. 214].

*Prodissopsalis eocaenicus Matthes 1952, p. 206 [= *Imperatoria gallwitzi* Matthes 1952, p. 214; = *Imperatoria hageni* Matthes 1952, p. 220; = *Geiselotherium robustum* Matthes 1952, p. 228]. Middle Eocene, Lutetian; Germany.

Prodissopsalis phonax, new species. Middle Eocene, Lutetian; Switzerland.

Prodissopsalis theriodis, new species. Middle Eocene, Lutetian; Switzerland.

Paracynohyaenodon Martin 1906, p. 424.

*Paracynohyaenodon schlosseri Martin 1906, p. 426. Late Eocene, Ludian; France.

?*Metasinopa* Osborn 1909, p. 423.

Metasinopa ethiopica (Andrew 1906, p. 233). Late Eocene, lower Fluvio-marine beds; Egypt. See also Schlosser (1911, p. 77), Van Valen (in press).

*Metasinopa fraasi Osborn 1909, p. 423. Early Oligocene, upper Fluvio-marine beds; Egypt. See also Schlosser (1911, p. 77).

Propterodon Martin 1906, p. 455.

*Propterodon morrisi (Matthew and Granger 1924, p. 1) [= *P. irdinensis* Matthew and Granger 1925, p. 4]. Late Eocene, Irdin Manha Formation; Mongolia. See also Van Valen (in press).

cf. *Propterodon*

Propterodon minutus (Douglass 1901, p. 19). Early Oligocene, Chadronian; Montana. See also Matthew (1903, p. 208), Scott and Jepsen (1936, p. 53), Van Valen (in press).

Dissopsalis Pilgrim 1910, p. 64.
  **Dissopsalis carnifex* Pilgrim 1910, p. 64 . Early Pliocene, Chinji beds, West Pakistan. See also
    Pilgrim (1914, p. 267), Pilgrim (1932, p. 11), Colbert (1933, p. 1), Colbert (1935, p. 75).
  ?*Dissopsalis ruber* Pilgrim 1910, p. 64. Locality and references as for *D. carnifex.*

Quercitherium (not *Quercytherium*) Filhol 1880, p. 48.
  * *Quercitherium tenebrosum* Filhol 1880, p. 48. Late Eocene, Ludian; France. See also Filhol
    (1882, p. 30; reprint of Filhol 1880), Filhol (1892, p. 135), Martin (1906, p. 429), Depéret (1917,
    p. 165), Piveteau (1935, p. 84), Russell and McKenna (1961, p. 277); Van Valen (in press).

The following genus and species have most recently been referred to the Proviverrini (as a subfamily or family) but are here not recognized as such:

Galethylax Gervais 1850. The type specimen is of uncertain relationships but is apparently not a pro-
    viverrine. See Van Valen (in press).
Proviverra americanus (*sic*) Scott 1892, is an artiodactyl (cf. Van Valen, in press).

The foregoing classification has a number of innovations, in addition to the new taxa. These may be summarized as follows. The type species of *Sinopa* is placed in *Proviverra* and other species are placed in *Proviverra* and three other genera. *Prototomus* is provisionally revived; it is probably a senior synonym of *Protoproviverra*. *Pseudosinopa* is synonymized with *Cynohyaenodon*, and *Prorhyzaena*, *Geiselotherium*, and *Leonhardtina* are synonymized with *Proviverra*; the synonymy of species in *Proviverra* is also new. *Geiselotherium robustum* is synonymized with *Prodissopsalis eocaenicus*, *Cynohyaenodon minor* is transferred to *Proviverra*, and *Paracynohyaenodon morrisi* is made conspecific with *Propterodon irdinensis*. *Propterodon* does not include the species on which it was originally based; see below.

GENERIC DIAGNOSES

The lower dentition is known for all species of proviverrines, but the upper dentition is unknown in a number of species. For this reason I will emphasize characters of the lower teeth. The skull, most of which is unknown in several genera, does not as yet provide characters that are clearly diagnostic at the generic level except for *Quercitherium* and *Dissopsalis*, genera that are recognizable at a glance from the teeth. All relative statements used in the diagnoses can be interpreted from published figures of the genera involved.

Prototomus, as tentatively used here, is known mainly from American species. It is the most primitive known genus of proviverrines and was probably the stem genus of the entire family Hyaenodontidae. For this reason the allocation of some species to *Prototomus* or other genera is arbitrary. Intergradation is particularly evident on the basis of species now known with *Tritemnodon*, which is, however, generically distinct at least by the middle Eocene. In the lower molars of *Prototomus* the metaconid is not or is only slightly reduced; it is larger than or equal to the paraconid, and may be considerably larger. The paraconid is not shifted anteriorly. The labial height of the protoconid above the talonid is about the same as the length of the trigonid. The molar talonids are two-thirds to fully as long as the trinonids, and the talonid rim is high or moderately high. The size of the trigonid of M_1 is less than or usually equal to that of M_2, which is about the same as that of M_3 but may be somewhat larger or smaller. The existence and length of diastemata between the canine and P_3 are variable. P_3 is relatively narrow and high:

its width is about a third of its length, and its labial height (above the base of the enamel on the roots) is two-thirds to four-fifths its length. The paracone and metacone of the upper molars are more or less close together but are not twinned, and are of about the same size as each other on M^1 and M^2 (either may be slightly larger). The European species *P. palaeonictides* is distinguished especially by the low angle (about 60°) that the posterolingual corner of the trigonid of at least M_1 makes with the horizontal plane of the tooth, and the fact that the metaconid of at least M_1 is about as tall as the protoconid when the sides of the trigonid are taken as vertical; one or occasionally both of these characters are present also in some American specimens.

Arfia has M_1 and M_2 with structure similar to that of *Prototomus*, but on M_3 the metaconid is moderately reduced and is somewhat smaller than the paraconid, which has shifted anteriorly to a variable degree. The M_3 protoconid height is variable with respect to the trigonid length. The molar talonids vary from as long as the trigonids to a little over half that length; their rims are high on M_1 and M_2, but reduced on M_3. The trigonid of M_3 is much larger than that of M_2, which is moderately larger than that of M_1. There are no diastemata or only one short one between the canine and P_3. P_3 is moderately wide and high; its width is two-fifths to half its length and its height is four-fifths of its length. The paracone and metacone of the upper molars are about as separated as in *Prototomus* and are of about equal size on M^1 and M^2. P^4 differs from that of all other proviverrines for which the upper dentition is known except *Quercitherium* in the reduction of the metastyle, which is a weak crest not more than a fifth of the labial length of the tooth.

Tritemnodon has lower molars with the metaconid slightly to (middle Eocene) much reduced; at least on M_3 the metaconid is smaller than or equal to the paraconid, and is almost always smaller. The paraconid is not to moderately shifted anteriorly. The labial height of the protoconid above the talonid is greater than or equal to the length of the trigonid, distinctly greater in the middle Eocene. The molar talonids are half to three-fourths as long as the trigonids in the early Eocene, not more than a third as long in the middle Eocene. The talonid rim, moderate to high in the early Eocene, becomes much reduced. The trigonid of M_1 is smaller than that of M_2, which is about the same size as that of M_3 but may be slightly larger or smaller. There are moderate diastemata between the canine and P_3. P_3 is narrow and low: its width is one-third to two-fifths of its length and its height is three-fifths of its length. The paracone and metacone of the upper molars are moderately to (middle Eocene) highly connate; the paracone is larger than the metacone, considerably larger in the middle Eocene.

Proviverra has a lower dentition like that of *Prototomus*; the molar talonids are sometimes even longer than the trigonids. The only consistent structural difference I have found between the genera, if they are regarded as distinct, is the greater separation of the paracone and metacone in *Proviverra*.

Cynohyaenodon has lower molars with the metaconid slightly to moderately reduced and the paraconid moderately to not shifted anteriorly. The M_3 protoconid height is slightly less than the trigonid length. The talonids are two-fifths to two-thirds the length of the trigonids, and have moderately high rims. The trigonids increase moderately and regularly in size from M_1 to M_3. There are no diastemata in the premolar region. P_3 is relatively wide and high: its width is about half its length and its height is about four-fifths its length (three-fifths in *C. trux*). The paracone and metacone of the upper molars

are only moderately (Lutetian) to closely appressed and are similar to each other in size on M^1 and M^2.

Prodissopsalis has the metaconid of the lower molars moderately to much reduced, it being smaller than the paraconid, which has shifted far anteriorly. The protoconid of M_3 is somewhat lower than the length of the trigonid. The talonids are a third to a half the length of the trigonids, and have low or intermediate rims. There is a moderate and progressive increase in the size of the trigonids from M_1 to M_3. Diastemata are absent. P_3 is relatively wide and low: its width is about half its length and its height is about three-fifths its length. The paracone and metacone of the upper molars are only moderately close together; the metacone is distinctly larger than the paracone on M^1 and M^2.

Paracynohyaenodon has the metaconid of the lower molars only slightly reduced on M_1 and M_2, moderately reduced on M_3. The paraconid is moderately to far anterior; the height of the protoconid of M_3 is probably about the same as the trigonid length. The talonids are half to two-thirds of the trigonid length, and have moderate to high rims. The trigonid of M_1 is moderately smaller than that of M_2, which is much smaller than that of M_3. The nature of the anterior and upper dentition is unknown.

Metasinopa is not certainly distinct at the generic level from *Paracynohyaenodon*. The metaconid of the lower molars is much reduced on M_1 and M_2, and nearly absent on M_3. The paraconid is moderately to far anterior; the height of the protoconid of M_3 is about the same as the trigonid length. The talonids are a third to a half the trigonid length, and have moderately high rims (at least on M_2). The trigonid of M_1 is moderately smaller than that of M_2, which is much smaller than that of M_3. Diastemata are absent. The P_3 is wide, its width in *P. fraasi* being about three-fifths its length. The height of P_3 and the nature of the upper dentition are unknown.

Propterodon has much reduced metaconids on the molars, and the paraconid is far anterior. The height of the protoconid of M_3 is unknown, but by analogy with M_1 and M_2 would be about the same as the trigonid length, perhaps slightly less. The talonid of M_1 is about four-tenths the length of the trigonid, that of M_2 three-tenths, and that of M_3 one-tenth. The talonid rim is moderately high labially and posteriorly, but is absent lingually. There is a considerable but regular increase in the size of the trigonid from M_1 to M_3. There are no diastemata in the premolar region. P_3 is relatively wide and high: its width is half its length and its height is four-fifths its length. The paracone and metacone of the upper molars are unknown.

Dissopsalis has the metaconid of M_1 moderately reduced, that of M_2 much reduced, and that of M_3 absent. It should be noted that the only known M_1 is from a different individual than the M_2 and M_3. The paraconid of M_1 is only slightly shifted anteriorly, while that of M_2 and M_3 is far anterior. The protoconid of M_3 is incompletely known but was probably considerably lower than the length of the trigonid. The talonid of M_1 and M_3 is about half the length of the trigonid, while that of M_3 is less than a fifth. The talonid rim is high or moderately high on M_1 and M_2, and nearly absent on M_3. The trigonid of M_2 is somewhat larger than that of M_1, and that of M_3 is considerably larger than that of M_2. The lower premolars anterior to P_4 are unknown, but by analogy with the maxilla there were probably one or two diastemata. P_4 is relatively wide. The paracone and metacone of the upper molars are not particularly close together; the paracone is much smaller than the metacone on M^1 and especially M^2. The greatly enlarged anteroposterior shearing surface on M^2 is diagnostic.

Quercitherium is immediately recognizable by its greatly enlarged and bulbous premolars, especially the second, which are larger than the molars. The metaconids of M_2 and M_3 are only slightly reduced; that of M_1 has not been described. The paraconids of M_1 and M_2 are not or are only slightly shifted anteriorly, while that of M_3 is moderately far anterior. The protoconid of M_3 is considerably lower than the length of the trigonid. The talonids of M_1 and M_2 are two-thirds to three-fourths the length of the trigonid, while that of M_3 is more or less a third the trigonid length. The talonid rim is high on at least M_1 and M_2. There is a moderate and progressive increase in the size of the trigonids from M_1 to M_3. Diastemata are absent. P_3 is tall and very wide: its width is about two-thirds its length and its height is about four-fifths its length. The paracone and metacone of the upper molars are not particularly close together; the paracone is smaller than the metacone on M^1 and especially M^2.

ADAPTATION, PHYLOGENY, AND PARALLELISM

Of the genera here included in the Proviverrini, only *Dissopsalis*, *Propterodon*, and *Metasinopa* are derivable from any other genus (except *Prototomus*) without invoking a reversal and subsequent re-establishment of carnassial specialization. The major criterion I use for a genus in proviverrines (aside from probable monophyly) is a significant difference in adaptive specializations from the most recent possibly ancestral genus.

Prototomus may be regarded as a primitive proviverrine in all characters. *Quercitherium* is specialized in its crushing premolars (with concomitant changes in the skull and mandible), with moderate carnassial specialization in the anterior paraconid of M_3 and the size of the metacone of M^2. *Proviverra* has somewhat less carnassial specialization than *Prototomus*. This difference is not great and is perhaps not of generic rank, but it represents a definite trend in opposition to that of all other proviverrines. *Proviverra minor* (Filhol) has crushing premolars, but these are not as large as those of *Quercitherium* and there are no indications of the carnassial specialization of the latter genus; in fact the molars of *P. minor* (Filhol) are nearly inseparable from those of *P. typica*. It is possible that the European and American species of *Proviverra* are independent developments from the stage of *Prototomus*, but this is simply speculation. Even evolutionary classification must follow the dictates of static morphology until reasonable evidence for a phylogeny is available.

At least five of the remaining eight genera present an interesting picture of independent adaptations to increase the efficiency of shear between the upper and lower molars. Each of the five has one or more specializations that are not present in any of the other four genera taken individually, although a single specialization may not distinguish a genus from all the other four genera taken together. This pattern is in fact an important reason for my recognizing these groups as genera.

Arfia is characterized especially by the enlargement and specialization of M_3 without particular carnassial specializations on the other lower teeth. *Tritemnodon* has tall trigonids with much reduced metaconids and talonids, moderately anterior paraconids, and connate paracone and metacone with the metacone reduced. *Cynohyaenodon* has only moderately reduced metaconids and talonids and moderately anterior paraconids, but has connate paracone and metacone by the Ludian. *Prodissopsalis* has reduced metaconids and anterior paraconids as its main specializations. *Paracynohyaenodon*,

as yet known from only one specimen, has a relatively anterior paraconid and an enlarged M_3; the metaconid of M_3 is less reduced than that of *Arfia*.

Metasinopa could have evolved from either *Arfia* or an early *Paracynohyaenodon*. It is similar to the latter, differing especially in its more reduced metaconids. The metaconid of M_3 of at least most specimens of *Arfia* is smaller than that of *Paracynohyaenodon* even in the Gray Bull. *Propterodon* could have been derived most easily from either *Cynohyaenodon* or *Prodissopsalis*; it is advanced in all known respects except that the M_3 is not notably enlarged. *Dissopsalis* seems almost equally well derivable from *Prodissopsalis* (perhaps the most likely candidate), *Paracynohyaenodon*, *Metasinopa*, Lutetian species of *Cynohyaenodon*, or even *Arfia*. It should, however, be noted that the upper teeth of *Paracynohyaenodon* and *Metasinopa* are unknown. The three genera discussed in this paragraph could easily have originated directly from *Prototomus* via unknown intermediates. The phylogeny of hyaenodonts is poorly known, and parallelism is so prevalent in demonstrable cases that it very possibly occurred in cases in which it cannot now be shown.

This last conclusion is particularly relevant to the Hyaenodontini (*Pterodon, Hyaenodon, Hempsalodon, Metapterodon, Ischnognathus,* and just possibly *Apterodon*, a probable mesonychid). The Hyaenodontini is defined exclusively on the basis of the degree of carnassial specialization, and it seems probable that the threshold was reached more than once. In particular, it is difficult to see how *Metapterodon* could have evolved from an ancestor in the Hyaenodontini. Even the genera *Pterodon* and *Hyaenodon* are defined largely on the basis of degree of carnassial specialization, and polyphyletic origin of them would not be surprising (but it is not yet proved). The ancestors of the Hyaenodontini are unknown, although *Prodissopsalis, Cynohyaenodon,* or an early *Propterodon* are probably the most likely candidates among described genera; *Metasinopa* is also quite possible. One or more species from the middle Eocene of Egerkingen ('*Hyaenodon*' *schlosseri* and others not certainly distinct) are already of the hyaenodontine grade; '*H.*' *schlosseri* lacks a metaconid of M_3 and the talonid is nearly absent on this tooth. It is probable that *Tritemnodon*, at least by the Bridgerian, was too divergent to give rise to any other known genus.

EGERKINGEN PROVIVERRINI

The geology of the fissure-fillings of Egerkingen has been summarized by Stehlin (1903, 1905). J. Hürzeler, who has also collected there, kindly provided some additional information. Three localities have been collected from since 1896; these are designated α, β, and γ. Quarries α and β are of late Lutetian age, while γ is of early or middle Lutetian age. The specimens collected before 1896 are largely or entirely from the early and middle Lutetian. I found only one specimen of a proviverrine (of *Prototomus torvidus*, from β) which was from either α or β; presumably all the species described here were nearly or quite contemporaneous, despite their number. One or more species of miacid and one or two of a form resembling the Hyaenodontini are also present in Egerkingen γ. The latter species are probably not referable to a described genus (cf. Martin, 1906). My schedule, arranged in advance under the belief that there were only about two species of Egerkingen proviverrines, was inflexible and did not permit complete analysis of the available material at Basel. It nevertheless seems desirable to present the information

obtained. The species were first distinguished on the basis of the upper dentition; the separation so obtained was confirmed by the lower dentition. Upper and lower teeth are referred to the same species on the basis of size, degree of carnassial specialization, and direct occlusal manipulation. There is only one mandible for *Prodissopsalis phonax*; in all other cases several to many specimens are available for both upper and lower dentitions.

<p style="text-align:center">*Proviverra typica* Rütimeyer</p>

<p style="text-align:center">Text-figs. 1B, 2A, 3A, 4A</p>

Proviverra typica Rütimeyer 1862, p. 80.
Prorhyzaena egerkingiae Rütimeyer 1891, p. 105.

Discussion. This species is the smallest and most abundant Egerkingen proviverrine. It is moderately although not excessively variable; this variation was regarded by Rütimeyer (1891) as indicating the presence of two species and even of two genera. No specimen in the Basel Museum labelled *Prorhyzaena* gives any indication of the structure of the premolars anterior to P^4, and from Rütimeyer's figure (1891) this has probably always been true despite statements about them in the literature. P^4 is not enlarged; that of the type of *Prorhyzaena egerkingiae* differs from that of the type of *Proviverra typica* mainly in the presence of two cuspules rather than one on the lingual lobe. The talonid of M_1 is as wide as the trigonid. The widest part of P_3 is just posterior of the middle. The alveolar length from the posterior end of the upper canine to the posterior end of P^4 is 18·0 and 17·7 mm. on the two sides of the type; to the posterior end of M^3 it is 28·3 mm.

Rütimeyer's various figures of the teeth are highly inaccurate. His partly corrected figures of the somewhat crushed skull (Rütimeyer 1862, pl. 5) are better, but the skull was probably somewhat deeper; text-fig. 3A of the present paper supplements them. The type skull of *P. typica* now contains the root of the right canine, the base of the crown of the left P^1, all of both P^4s, both M^1s without most of the paracone and metacone and the distal end of the metacrista, the lingual half of the right M^2, and the left M^3 without the surface of the crown of the labial half.

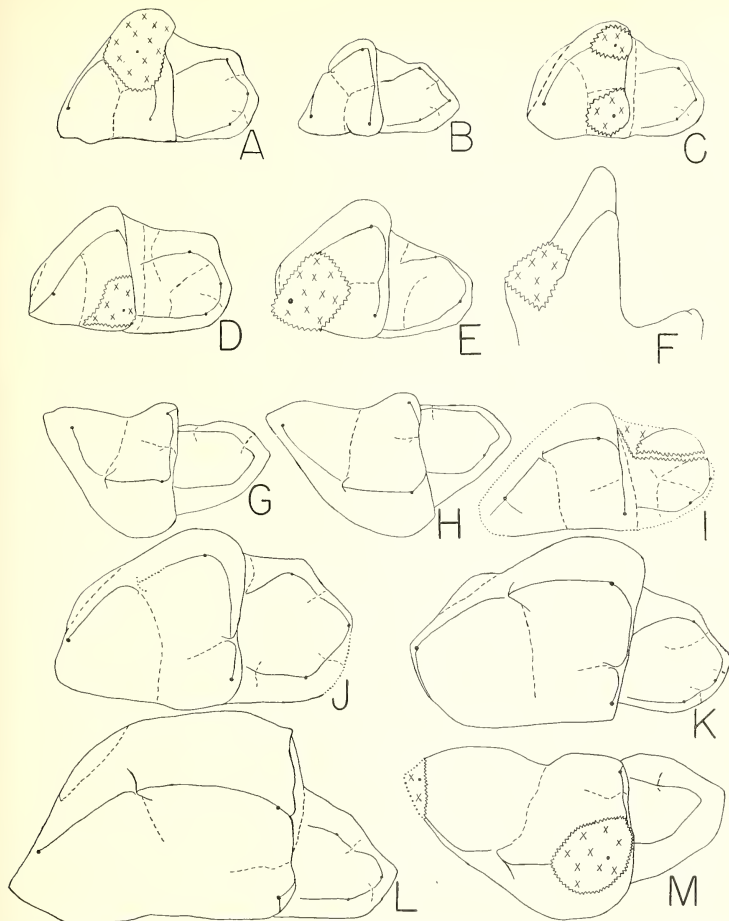<p style="text-align:center">*Prototomus torvidus* sp. nov.</p>

<p style="text-align:center">Text-figs. 1A, 4B</p>

Type. NMB No. Eh. 522, partial right maxilla. See text-fig. 4B.

Type locality. Egerkingen γ.

Diagnosis and discussion. *P. torvidus* is slightly more carnassial than *Proviverra typica*, but the two species may nevertheless be congeneric. *Prototomus torvidus* is somewhat larger. In the upper molars the main differences are that the protocone of *Prototomus torvidus* is lower and the metacrista is taller than in *Proviverra typica*; the paracone and metacone are also closer together and taller. M^3 is moderately reduced in *Prototomus torvidus* but not in *Proviverra*. The protocone lobe of the P^4 of *Prototomus torvidus* is distinctly shorter anteroposteriorly than that of *Proviverra typica*, and lacks or nearly lacks cuspules on its lingual rim except for the protocone; in *Proviverra typica* there are usually rather prominent cuspules there. The metacrista of P^4 is cut off from

TEXT-FIG. 1. Lower molars of proviverrines, mainly in occlusal view. A, *Prototomus torvidus*, NMB unnumbered, right M_3, ×6·8. B, *Proviverra typica*, NMB unnumbered, right M_3, ×6·8. C, *Proviverra minor* (Filhol), NMB No. Q.C. 1028, right M_3, ×6·8. D–F, *Proviverra gracilis*, MME No. 343, ×6·0 D, occlusal view right M_2; E, occlusal view right M_3; F, lingual view right M_3. G, *Cynohyaenodon trux*, NMB unnumbered, left M_3, ×6·8. H, *Cynohyaenodon ruetimeyeri*, NMB unnumbered, left M_3, ×6·8. I, cf. *Prodissopsalis sp.*, MME No. 3987, unerupted right M_2, ×6·0. J–K, *Paracynohyaenodon schlosseri*, type, NMB No. Qu. B. 393, ×6·8. J, right M_2; K, right M_3. L, *Prodissopsalis theriodis*, NMB No. Em. 14, right M_3, ×6·8. M, *Prodissopsalis phonax*, NMB unnumbered, left M_3, ×6·8. In all text-figures dotted lines are inferred, dotted regions are wear surfaces, dashed lines are valleys, large dots are cusp apices, and jagged lines and regions with X's are broken.

the paracone by a sharp carnassial notch; they do not more or less merge as in *Proviverra typica*. The parastyle of P⁴ is somewhat wider also, causing the deep notch in the anterior border of the tooth to be about central rather than distinctly on the labial half of the tooth as in *Proviverra typica*. In the lower molars the talonid and metaconid of *Prototomus torvidus* are relatively slightly smaller than in *Proviverra typica*, but the metaconid is still larger than the paraconid in lingual view. There is a reasonable possibility that *Prototomus torvidus* belongs to *Proviverra* even if *Prototomus* is generically distinct from *Proviverra*, but it is placed in *Prototomus* pending clarification of the early Eocene proviverrines of Europe.

The specific name is a Latin word meaning savage or wild, in allusion to the presumably predaceous habits of the species and also with reference to the work of R. J. G. Savage on the Old World Hyaenodontidae and that of D. E. Savage on the European Eocene.

Cynohyaenodon trux sp. nov.

Text-figs. 1G, 2B, 3B

Type. Unnumbered fragment of rostrum in Naturhistorische Museum, Basel. See text-fig. 3B.

Type locality. Egerkingen, quarry unknown.

Diagnosis and discussion. The paracone and metacone of the upper molars are much more separate than in *C. cayluxi* (the upper molars of *C.? leenhardti* are unknown), being intermediate in this respect between those of *Prototomus torvidus* and *Proviverra typica*. The protocone lobe of the upper molars is slightly shorter anteroposteriorly than in *Proviverra typica*; the protocone is relatively low and the metacrista is relatively high and long, as in *Prototomus torvidus*. The protocone lobe of P⁴ is distinctly longer anteroposteriorly than that of *Prototomus torvidus*, being similar in this respect to that of *Proviverra typica*, but this lobe is narrow transversely and extends anteriorly nearly as far as does the parastyle. The notch in the anterior border of P⁴ is shallow and central; the nature of the metacrista is unknown. P³ has a third root in at least the type, unlike at least *Proviverra typica*. The metaconid of M₃ is moderately reduced and the paraconid is moderately anterior, and the cusps of the talonid are more or less merged into the talonid rim, unlike the situation in *Proviverra* and *Prototomus*. M₁ is not quite as tall as M₂. The paraconid of P₄ is relatively smaller than that of *Proviverra typica* but the talonid is relatively larger. The height of P₃ is much less than that of M₁. P₂ is taller than P₃; the apex of the protoconid of P₂ is about a third of the distance from the anterior end of the tooth. P₄ is widest at the talonid; P₃ is widest just anterior of the talonid. The alveolar length from the posterior end of the upper canine to the posterior end of P⁴ on the type of 25·2 mm.

The specific name is a Latin word meaning savage or fierce, given for the same reasons as *Prototomus torvidus*.
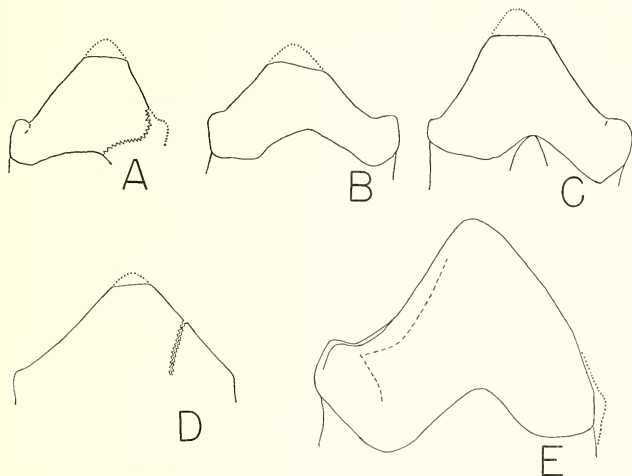
Cynohyaenodon ruetimeyeri (Depéret)

Text-figs. 1H, 2C, 4C

Type. The mandible figured by Rütimeyer (1891) in his plate 7, fig. 10, is here designated as the type. It is in the Naturhistorische Museum, Basel.

Diagnosis and discussion. The upper molars of *C. ruetimeyeri* are rather similar to those

of *C. trux*, but are somewhat larger and the protocone lobe is slightly smaller. The protocone lobe of P^4 is more transverse than in the three Egerkingen species described above, and also slightly more transverse than in *C. cayluxi*. It does not extend far anteriorly. The notch in the anterior border of P^4 is moderately deep and distinctly on the labial half of the tooth. As in *C. cayluxi*, there is a distinct carnassial notch between the metacrista and the paracone. The embrasure pit (a pit in the maxilla in the embrasure


TEXT-FIG. 2. P_3 of proviverrines, labial view. A, *Proviverra typica*, NMB unnumbered, right P_3, ×6·8. B, *Cynohyaenodon trux*, NMB unnumbered, left P_3, ×6·8. C, *Cynohyaenodon ruetimeyeri*, NMB unnumbered, ×6·8. D, *Proviverra gracilis*, MME No. 343, left P_3, ×6·0. E, *Prodissopsalis theriodis*, NMB unnumbered, ×6·8. Symbols as in text-fig. 1.

between two cheek teeth) between M^2 and M^3 is about the same size as that between M^1 and M^2, which is concordant with the fact that the trigonid of M_3 is not much larger than that of M_2. The paraconid of the lower molars is somewhat more anterior than in *C. trux*, the metaconid is somewhat smaller, and M_1 is somewhat more reduced. The paraconid is somewhat further forward and the metaconid slightly smaller than in *C. cayluxi*. The lower premolars are considerably wider and more robust than in *C. trux*. P_4 is of about equal width at the middle and the talonid; P_3 is widest in the middle or just posterior of the middle. P_3 is considerably larger relative to P_4 than in *C. trux*; the height of P_3 is almost equal to that of M_1. As in *C. trux*, the height of P_4 is greater than that of M_1 but less than that of M_2.

Depéret (1917, p. 172) casually established the genus and species *Pseudosinopa rutimeyeri*, relying on Rütimeyer's figures. The two jaws mentioned as belonging to this

species are those figured by Rütimeyer (1891) in his plate 7, figs. 10 and 11. Both specimens figured there are reversed as to the side of the mouth. On comparison of these jaws with the other specimens of Egerkingen proviverrines, it became evident that
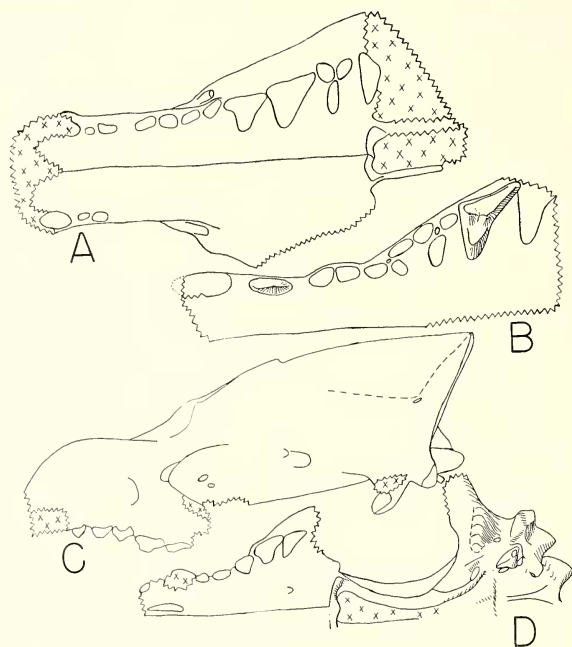
TEXT-FIG. 3. Proviverrine skulls, not drawn with reticule. A, *Proviverra typica*, type, ventral view of rostrum with outlines of some alveoli and left P^4, M^1, and M^3; ×2·0. B, *Cynohyaenodon trux*, type, ventral view of rostrum with P^1, M^1, and outline of M^2, ×2·0. C–D, *Prodissopsalis theriodis*, type, NMB No. Em. 12, ×0·5. Left side and ventral view of left half of skull, with outlines of P^1–M^1; additional orbital foramina may also be present. Symbols as in text-fig. 1.

the specimen of Rütimeyer's fig. 10 is specifically and even generically different from that of his fig. 11, which belongs to *Prodissopsalis phonax*. As both the names *Prodissopsalis* and *Cynohyaenodon* are in current use while *Pseudosinopa* is not, I have restricted the type of *P. ruetimeyeri* to the specimen of the older genus to preserve the current names. The spelling of the specific name is altered because the species was named after Rütimeyer.

Prodissopsalis phonax sp. nov.

Text-figs. 1M, 4D

Type. NMB No. Em. 16, partial skull. See text-fig. 4D.

Type locality. Egerkingen, quarry unknown.

Diagnosis and discussion. The protocone of the upper molars is slightly smaller than that of *Prototomus torvidus* and *Cynohyaenodon trux*. The paracone and metacone are only moderately connate. The protocone of P^4 and the upper molars is somewhat more anterior and lower and relatively slightly smaller than that of *Cynohyaenodon ruetimeyeri*. The paracone is slightly smaller relative to the metacone, and these cusps are usually slightly more connate than in *C. ruetimeyeri*. The embrasure pit between M^2 and M^3 is distinctly deeper than that between M^1 and M^2, which corresponds with the fact that the trigonid of M_3 is considerably larger than that of M_2. M_1 is slightly more reduced in comparison to that of *C. ruetimeyeri*, and M_3 is somewhat taller relative to M_2. The paraconid is considerably more anterior, the metaconid is somewhat smaller, and the horizontal ramus is somewhat deeper and thicker than in *C. ruetimeyeri*.

In the type skull the postvallum of M^2 is almost entirely worn away; most of the metacone has been removed in the process. There is virtually no wear on the postvallum of P^4 or M^1, although the cusps of these teeth are somewhat worn from the apices. This wear pattern emphasizes the importance that M^2–M_3 shear had attained in *Prodissopsalis*. The skull is apparently somewhat deeper than that of *Proviverra*. The orbit extends only to the anterior part of M^1, not to the posterior part of P^4 as in both American and European species of *Proviverra*.

The species *Cynodon helveticus* Rütimeyer 1862, was founded on an isolated lower molar and has been variously referred to the Canidae and the Miacidae. The specimen in the Basel Museum now labelled as the type belongs to *Prodissopsalis phonax*. I do not regard the two species as necessarily synonymous, because the tooth mentioned is of a different size and morphology from the type of *C. helveticus* (or else, as is possible, the published measurement is ten per cent. off and the figure is quite unrecognizable). I have therefore proposed to the International Commission on Zoological Nomenclature that the name *Cynodon helveticus* be suppressed.

The specific name of *P. phonax* is a Greek word meaning bloodthirsty, given for the same reasons as *Prototomus torvidus*.

Prodissopsalis theriodis sp. nov.

Text-figs. 1L, 2E, 3C–D, 4E–G

Type. NMB No. Em. 12, nearly complete skull. See text-figs. 3C–D, 4E.

Type locality. Egerkingen, quarry unknown.

Diagnosis and discussion. The upper molars differ from those of *P. phonax*, aside from greater size, in having a somewhat longer metacrista. The upper and lower premolars are broader and more bulbous than those of *P. phonax*. The only structural difference in the lower molars is that in most specimens the talonid is relatively smaller in
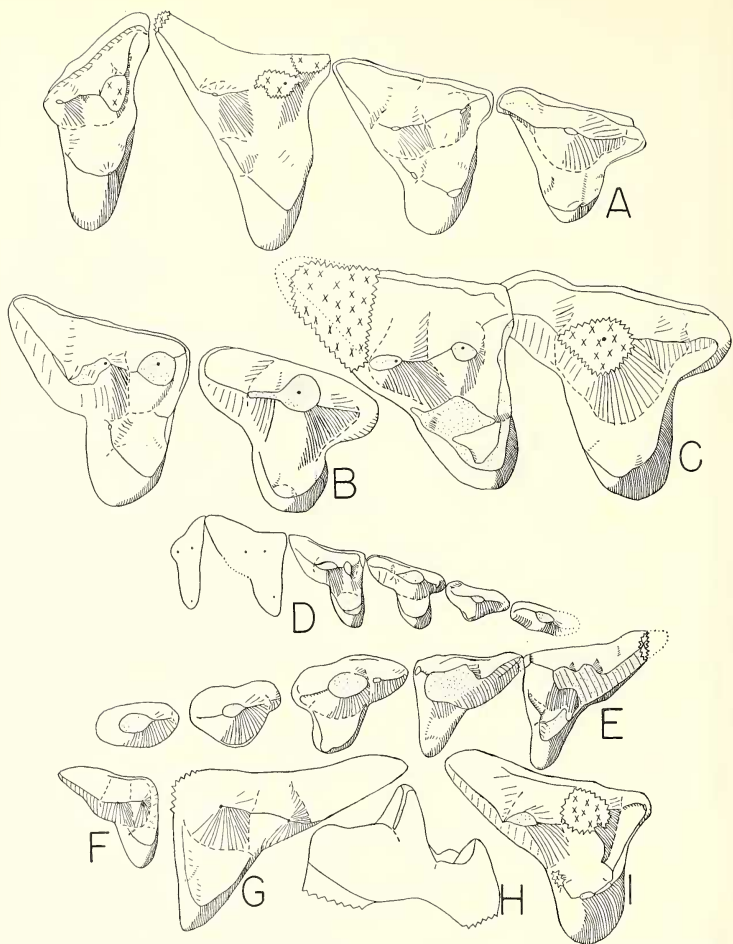
TEXT-FIG. 4. Upper cheek teeth of proviverrines, mainly in occlusal view. A, *Proviverra typica*, right P⁴ (from type), M¹ (NMB, unnumbered isolated tooth), M² (NMB, unnumbered maxilla with P⁴–M³), and M³ (NMB No. Eh. 554), all ×6·8. B, *Prototomus torvidus*, type, NMB No. Eh. 522, right P⁴–M¹, ×6·8. c, *Cynohyaenodon ruetimeyeri*, NMB unnumbered, right P⁴–M¹, ×6·8. D, *Prodissopsalis phonax*, type, NMB No. Em. 16, right P²–M¹ and outlines of M²⁻³, ×2·0; not drawn with reticule. E–G, *Prodissopsalis theriodis*; not drawn with reticule. E, left P²–M¹ (type, NMB No. Em. 12) and M² (NMB unnumbered), all ×2·0. F, right M¹ (NMB, unnumbered DP⁴–M¹), ×2·0. G, left M² (NMB, unnumbered), ×3·2. H–I, *Prodissopsalis sp.*, NMB No. Bchs. 266, right M⁷¹, ×6·8. H, direct posterior view; I, occlusal view. Symbols as in text-fig. 1.

P. theriodis; the horizontal ramus of the mandible is, however, relatively much deeper. The skull characters are as for *P. phonax*; it can be seen in *P. theriodis* that the infraorbital foramen is rather high and the basicranium is short relative to these structures in *Proviverra*. The embrasure pit between M^2 and M^3 is very deep, in correspondence with the tall trigonid of M_3. There is no evidence of a bulla.

Martin (1906) recognized that *P. theriodis* was generically distinct from all named forms, so he proposed the name *Propterodon* for it. Unfortunately he did not also propose a specific name, and by the vagaries of the rules of nomenclature *Propterodon irdinensis* is the type species of *Propterodon*. I believe that *Propterodon morrisi* (= *P. irdinensis*) is generically distinct from *Propterodon theriodis*, which thereby excludes *P. theriodis* from the genus originally based on it. The specimen figured by Rütimeyer (1891, pl. 7, fig. 15a) on which *Propterodon* was largely based, is clearly referable to *Prodissopsalis theriodis* despite the inaccurate rendition of M_3, the only tooth preserved. This inaccurate drawing led Matthew and Granger (1925) to believe that their *Propterodon irdinensis* was congeneric with *Prodissopsalis theriodis*. *P. theriodis* is different from '*Hyaenodon*' *schlosseri*, which is even more advanced. Stehlin (1940) mentions the presence in the late Ypresian Teredinasande (= sables à Unios) of Epernay, of a species related to *P. theriodis* but of greater size.

The name *theriodis* is a Greek word meaning savage, and is given for the same reasons as *Prototomus torvidus*.

GEISELTAL CARNIVORES

The geology and biota of the famous middle Eocene brown coal of Geiseltal have been well discussed by Krumbiegel (1959) and will not be repeated here. In 1952 Matthes described six genera and eight species of carnivores, all as new, from the Geiseltal. Two of the monotypic genera have elsewhere (Van Valen, in press, *b*) been transferred to the insectivore family Paroxyclaenidae and shown to represent only one species. I believe that only two genera and species are represented by the remaining named taxa, although as will be shown below there are also other carnivores present in the fauna.

The preservation of microscopic details in the Geiseltal material is justly famous but macroscopically the specimens of mammals are usually crushed so badly that, aside from the teeth, only the most obvious features of their anatomy can be determined. The photographs published by Matthes (1952) indicate most of what can be seen of the two species he discussed; the drawings in the present paper are meant only to supplement these photographs in regions which would otherwise be obscure. All the known specimens of Geiseltal carnivores are in the Museum für Mitteldeutsche Erdgeschichte, Halle/Saale.

The absence of any species of proviverrines in common between the faunas of Egerkingen and Geiseltal is somewhat surprising for neighbouring faunas supposedly of the same age. The ecology of a coal swamp is, however, presumably different from that of the Egerkingen fissures. No proviverrine species of either fauna is definitely more advanced than comparable species in the other fauna. The rarity of isolated teeth of small animals in the Geiseltal collection is perhaps due to the fact that the teeth are coloured shiny black like the matrix and are easily overlooked.

Proviverra gracilis (Matthes)

Text-fig. 2D

Leonhardtina gracilis Matthes 1952, p. 223.
Geiselotherium pilzi Matthes 1952, p. 225.

Diagnosis and discussion. Only the lower dentition of *P. gracilis* is surely known (see below). It is the largest known European species of *Proviverra*; the length of M_2 of two specimens is 6·1 and 6·4 mm. The structure of the lower molars is, as far as determinable, the same as that of *Proviverra minor* Filhol, but the premolars are narrow and not robust as in the latter species. P_3 is unusual for European species of *Proviverra* in that it is relatively low; it lacks a paraconid and talonid. P_4 also lacks a paraconid. One upper tooth from Leonhardt Quarry, MME No. 2832, is probably referable to *P. gracilis*. Its labial length is about 6·8 mm.; the protocone lobe is missing, as is the junction between the metacone and the metacrista. The paracone and metacone are of about equal size, and are separated to about the same degree as in *P. typica*.

The diagnoses of *Leonhardtina* and *Geiselotherium* given by Matthes (1952) do not clearly distinguish between them. The only character in the diagnoses that is apparently different, the relative height of the paraconid and metaconid on the lower molars, is a result of breakage in the type of *L. gracilis*. I have compared the types with each other and find no reason to regard them as of distinct species.

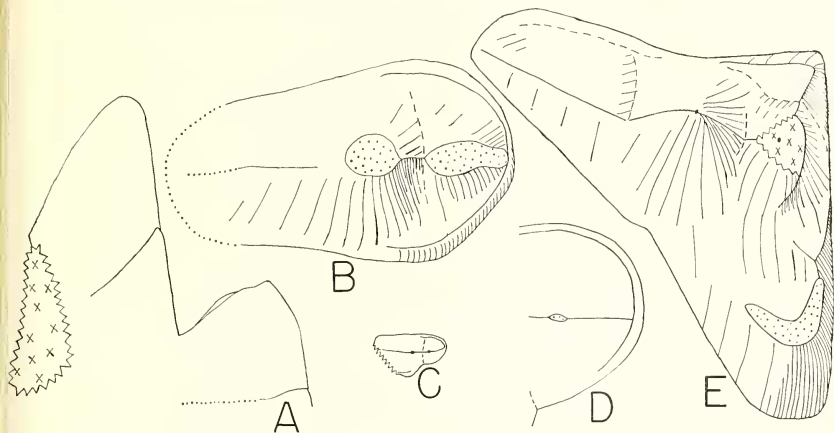*Prodissopsalis eocaenicus* Matthes

Text-figs. 5B–E

Prodissopsalis eocaenicus Matthes 1952, p. 206.
Imperatoria gallwitzi Matthes 1952, p. 214.
Imperatoria hageni Matthes 1952, p. 220.
Geiselotherium robustum Matthes 1952, p. 228.

Diagnosis and discussion. *P. eocaenicus* is most similar to *P. theriodis* but is considerably larger. In *P. eocaenicus* the metacrista of the upper molars is somewhat shorter, and the paracone and metacone are slightly more connate. The upper premolars are not clearly different when the total samples are considered except that the metastylar lobe of P^3 is somewhat larger in *P. eocaenicus*. The metaconid of the lower molars is slightly more posterior in *P. eocaenicus* and perhaps slightly smaller. The paraconid is also smaller and somewhat lower. A paraconid is present on the P_3 of *P. eocaenicus*; it is absent on the P_3 of *P. theriodis*.

The conspecificity of the upper dentitions (*P. eocaenicus* of Matthes) and the lower dentitions was determined by size, comparison with *P. theriodis*, morphological occlusal relations, and direct occlusal manipulation (allowing for crushing). The embrasure pit in the maxilla between M^2 and M^3 is larger than that between M^1 and M^2, and these are of the relative size expected with the M_2 and M_3 of the lower dentitions. Almost all the differences between the mandibles and lower teeth mentioned by Matthes (1952) are due to crushing, and the few remaining differences are of the magnitude expected in a relatively invariable species. Metrically, only two measurements could be taken on as many as six specimens: the diameter of the trigonid of M_3 from the anterolingual base of the paraconid to the posterolabial base of the protoconid, and the length of P^3.

The coefficients of variation (and the mean in parentheses) for these measurements are 2·8 (11·8) and 7·4 (12·6) respectively, both based on six specimens from two or three quarries. The upper jaws in fact differ more (in the structure of P^3 and in size) than do the lower jaws, but Matthes placed them in a single species and in this I follow him.

The degree of molarization of P^3 is somewhat variable in *P. eocaenicus*. In the type (MME No. 94) there is no trace of a protocone, while in MME No. 93 a distinct protocone lobe bearing a separate cingulum is present (text-fig. 5c). A third specimen, MME

TEXT-FIG. 5. A, cf. *Oxyaena sp.*, BM No. M13778, lingual view right $M_2 \times 5 \cdot 0$; not drawn with reticule. B–E, *Prodissopsalis eocaenicus*, not drawn with reticule. B, left P^3, type, occlusal view, $\times 5 \cdot 0$. C, left P^3, MME No. 93, occlusal view, $\times 1 \cdot 1$. D, metastylar lobe of left P^4, type, occlusal view, $\times 5 \cdot 0$. E, right M^2, paratype, occlusal view, $\times 5 \cdot 0$. Symbols as in text-fig. 1.

No. 3980, is intermediate. Presumably P^3 is about at the anterior limit of possible expression of the protocone prepattern.

The name *Prodissopsalis* has been chosen over *Imperatoria* by Savage (in press). I would have preferred the latter name to avoid phylogenetic commitments, and had in fact chosen it (Van Valen, in press), but Savage's choice may stand. The Egerkingen species *P. theriodis* is in fact somewhat more similar to *Dissopsalis* than is *P. eocaenicus*.

cf. *Prodissopsalis sp.*

Text-fig. 1I

One mandible, described by Heller (1930) as an oxyaenid and not mentioned by Matthes (1952), is not referable to either of the species described above. This specimen is MME No. 3987; no information is available as to which individual quarry yielded it. The specimen is one of the two specimens of proviverrines I can recall that have deciduous teeth; the other is the type of '*Paracynohyaenodon*' *morrisi*. DP_3 and DP_4 are

present, as is the unerupted and broken M_2. No evidence is available as to the presence or absence of M_3. The paraconid of M_2 is slightly lower than the metaconid. The trigonid is relatively higher than that of the M_2 of *Proviverra gracilis*, the protoconid is much longer, and the talonid is somewhat shorter. The paraconid is more anterior and relatively longer. The talonid cusps are more prominent than in *P. gracilis*, and the basin and grooves there are deeper. The prefossid (the depression in the trigonid) is a deep pit, whose bottom slopes only gradually down lingually.

There is a possibility that this specimen belongs to the Limocyonini, but such a placement is not made here. The ancestors of *Thereutherium*, the only known European limnocyonine, are as yet unknown, but it seems improbable that the species to which the present specimen belonged was ancestral because of its considerably greater size. Because it fits readily into *Prodissopsalis*, although not into any described species, this specimen is tentatively referred to *Prodissopsalis*. It is somewhat the smallest known species of that genus if correctly allocated; the length of M_2 is 7.2 ± 0.2 (approximate 95 per cent. confidence interval) mm., and the trigonid width of M_2 is 4.2 ± 0.1 mm.

Miacis? *macintyri* sp. nov.

Text-figs. 6A–C

Type. MME No. 3849.

Type locality. Geiseltal, quarry uncertain.

Diagnosis and discussion. A true miacid, not previously mentioned, occurs at Geiseltal. The type is a compressed skull with the upper and lower jaws nearly in occlusion, together with much of the skeleton. Without further preparation many diagnostic features are obscure, but enough is visible to show that an undescribed and interesting species is present.

The number of molars cannot yet be determined, but analogy with other species suggests that three will be found in each jaw. The full completement of four premolars is present. There is no parastyle on P^4; P^4 has a strongly tilted paracone. The labial cingulum of P^4 is incomplete, and the metacrista is highest anteriorly. The parastyle lobe of M^1 is moderately strong and projects anteriorly as well as labially. At least a precingulum is present on M^1; the presence of a postcingulum is uncertain. The paracone of M^1 is much larger than the metacone, and overhangs the anterior part of the tooth or nearly does so. The paracone and metacone are rather sharp, as is the centrocrista. The stylar shelf is relatively narrow, and there is no distinct metaconule. M^1 is relatively narrow transversely. The length of P^4 is 9.8 ± 0.1 (approximate 95 per cent. confidence interval) mm., the length of the labial border of M^1 is 7.8 ± 0.2 mm., and the slant height of the paracone of P^4 from the base of the enamel is 6.3 ± 0.2 mm.

I have compared my notes and drawings of *M.*? *macintyri* with the type of '*Viverra*' *hastingsiae* (probably the same as '*Viverravus*' *angustidens*, *fide* Teilhard 1915), BM No. 30203. The M^1 of the latter is more transverse than in *M.*? *macintyri*, the metacone is larger, the stylar shelf is wider, the parastyle projects more labially but less anteriorly, and lingual cingula are nearly absent. In labial view, the angle at the top of the paracone of M^1 is larger than in *M.*? *macintyri*. A definite parastyle is present on P^4, although it is weak; the paracone and metacrista are lower relative to the length of P^4; and there is a rather large cuspule in the position of a mesostyle, low and posterolabial of the

paracone. *Miacis invictus* Matthew and Granger (1925), from the Irdin Manha, is smaller and structurally different in several respects.

As far as I can determine, the species most similar to *M.? macintyri* is *M.? exilis* from the French Phosphorites. On this species see Teilhard (1915). For the upper dentition of *M.? exilis* only a poor photograph of the lateral view of the skull has been published. Teilhard's comments, however, refer to the two features that are the most striking in the upper dentition of *M.? macintyri*, namely the much reduced metacone and the beak-like parastyle. These points are of course only suggestive without further knowledge of both species. *M.? macintyri* is much larger than *M.? exilis*.
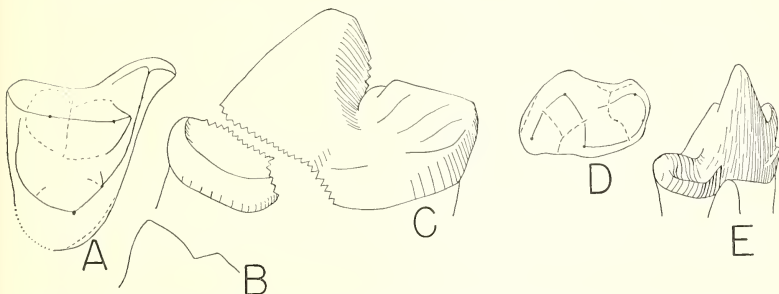
TEXT-FIG. 6. A–C, *Miacis? macintyri*, MME No. 3849. A, occlusal view right M¹, ×4·2, not drawn with reticle. B, labial view paracone and metacone of right M¹, ×4·2, not drawn with reticle. C, labial view right P⁴, ×6·0. D–E, *Eutheria* incertae sedis, MME No. 2833, ×6·0. D, occlusal view; E, directly labial view. Symbols as in text-fig. 1.

It is quite possible that *M.? macintyri* will not prove to belong to the genus *Miacis* when better known. It may be noted that the M₁ of *M.? exilis* differs from that of the American species in having a lower trigonid and a broader talonid. The M¹ of at least *M.? macintyri* is squat and is small in comparison to P⁴. Probably relevant miacid material from Egerkingen is preserved in quantity at Basel. The species name is after G. T. MacIntyre, who is revising the Miacidae.

cf. *Miacidae*, incertae sedis

A single upper tooth figured by Heller (1930, pl. 1, fig. 6) appears to be the P⁴ of a miacid, but it is not closely similar to any P⁴ known to me. I could not find this tooth when I was in Halle in 1963.

Eutheria incertae sedis

Text-figs. 6D–E

One isolated tooth, MME No. 2833, from Cecilie Quarry, is of peculiar morphology and is not closely similar to any other mammal with which I have compared it. It could be a P₄, a DP₄, or a molar. The talonid is relatively small and very low; its top is at the

same level as the base of the enamel on the lingual side of the trigonid. Talonid cusps are nearly absent. The posterior wall of the trigonid slopes far posteriorly, especially on the lingual side. A strong labial cingulum is present by the talonid. The length of the tooth is 4·2 mm., the trigonid width is 2·7 mm., and the slant height of the proto-conid from the base of the enamel on the anterior root is 3·7 mm.

When in Halle I regarded this tooth as the molar of a proviverrine descended from *Prototomus palaeonictides*, but this allocation seems rather improbable. Its least unlikely affinities seem to be as the DP_4 of an erinaceoid or the M_2 of a miacine. The P_4 or DP_4 of a paroxyclaenid (Van Valen, in press, *b*) is also a possibility.

REMARKS ON OTHER OXYAENOIDS

Proviverra minor (Filhol)

Text-fig. 1c

As noted above, the species described by Filhol (1877) as *Cynohyaendon minor* is referable to *Proviverra*. It is easily distinguishable from *P. typica* by the more bulbous premolars, but the molars are very similar. I could detect no consistent difference whatever in the upper molars. The lower molars of *P. minor* are slightly wider than those of *P. typica*, the talonid of M_3 (only) is slightly shorter, the paraconid of P_4 is relatively smaller, and the talonid of P_4 is slightly less developed lingually.

Prodissopsalis sp.

One upper molar (NMB No. Bchs. 266) from the Lutetian of Bouxwiller (Buchs-weiler), Alsace, is apparently referable to *Prodissopsalis*. It is probably a right M^1 and represents an undescribed species, being considerably smaller than *P. phonax* and structurally different as well. The parastyle is larger than in *P. phonax*, but the most important structural difference from the named species of the genus is in the relatively large size of the protocone, particularly its height. This is a primitive character, as is presumably the small size, and suggests that the Bouxwiller species is the most primitive of its genus. The protocone region is rather similar to that of *Oxyaena*. The wear pattern is, however, markedly different (cf. Van Valen, in press) and reference to the Proviver-rini seems necessary. The relatively small protocone lobe and the moderate separation of the paracone and metacone indicate reference to *Prodissopsalis* rather than to *Proto-tomus* or *Cynohyaenodon*. The length of the labial border is 5·8 mm., of the anterior border 4·5±0·1 (approximate 95 per cent. confidence limits) mm., and of the posterior border 6·8±0·1 mm.

cf. *Oxyaena sp.*

Text-fig. 5A

Three specimens possibly referable to *Oxyaena* are now known from the Blackheath Beds, probably of earliest Eocene age, at Abbey Wood, England. White (1931) has discussed the geology. The most diagnostic specimen is BM No. M13778, an unworn isolated M_2, from which the paraconid is missing. This tooth was figured inaccurately by Cooper (1932), who compared it especially with '*Sinopa*'. It differs from Wasatchian proviverrines especially by the fact that the hypoconid is slightly lower than the ento-

conid (cf. Van Valen, in press). The metaconid is about a third of the width of the protoconid. The width of the trigonid is 8·5 mm., the width of the talonid is 6·2 mm., the labial slant height of the protoconid from the base of the enamel on the anterior root is 13·9 mm., and the length (parallel to the base of the enamel) from the carnassial notch of the paralophid to the posterior end of the tooth is 11·0 mm. The second specimen, BM No. M15128, is the unworn protocone lobe of an upper molar, probably the M^1 of an oxyaenid. It differs from American species of *Oxyaena*, however, in having the lingual cingula, which are weak but joined lingually, definitely less than half the height of the protocone. Its anteroposterior length at the conules is 5·8 mm. A third specimen, BM No. M15125, is a $(D)P^3$ or $(D)P^4$ which is worn nearly to the roots. The protocone is weak and slightly anterior of the midline; there are weak lingual cingula, which are not joined on the lingual side of the protocone.

The only known specimen of *Argillotherium toliapicum*, from the London Clay, has recently been identified (Van Valen, in press) as very probably an immature oxyaenine, cf. *Oxyaena*. No additional specimens referable to the Oxyaeninae have been reported from Europe (Van Valen, in press). The lower molar of cf. *Oxyaena* from Abbey Wood is of an appropriate size for the skull of '*Argillotherium*', and is very possibly conspecific with it. BM No. M15125 could be the last permanent or deciduous premolar of this species. BM No. M15128 is, however, considerably too small to fit into the single molar alveolus in the type of '*Argillotherium*', and is probably at least specifically distinct. It is moreover not excluded that all three teeth from Abbey Wood are conspecific with each other and different from '*Argillotherium*'.

cf. *Prototomus sp.*

The presence of the Proviverrini in England is shown by a fragment of mandible with M_3, BM No. M20212, from the Blackheath Beds at Abbey Wood. The tooth is that of a primitive proviverrine. The lingual length is 4·7 mm., the trigonid width is 2·8 mm., the talonid width is 1·9 mm., and the labial slant height of the protoconid from the base of the enamel on the anterior root is 4·6 mm. It is probable that *Didelphis*? *colchesteri* Owen (1846) from Kyson (probably equivalent to or a facies of the Pebble-beds) is also a proviverrine and may represent the same species, although the type of *D.*? *colchesteri* may not be adequate for identification at the species level. On *D.*? *colchesteri* see also Charlesworth (1839), Lyell (1840), and Owen (1840); on the geology of Kyson see Prestwich (1850), Whitaker (1885), and White (1931). Prestwich (1850) and others ascribe the name *D.*? *colchesteri* to Charlesworth, but I have been unable to find a paper in which he uses this name.

Arfia gen. nov.

Type species. *Sinopa opisthotoma* Matthew 1901, p. 28.

Referred species. *Sinopa shoshoniensis* Matthew 1915, p. 73 (possibly a synonym of *A. opisthotoma*).

Diagnosis and discussion. *Arfia* differs from other proviverrines by the following characters: M_1 and M_2 unspecialized, metaconid of M_3 moderately reduced and paraconid of M_3 shifted anteriorly, M_3 enlarged, metacrista of P^4 much reduced. Further differences have been given above with the comparison of genera. The name is onomatopoeic. *Arfia* represents a distinct specialization among the Proviverrini and, although possibly

ancestral to *Paracynohyaenodon* or even *Quercitherium*, is sufficiently different from these and from *Prototomus* to necessitate a separate genus.

Metasinopa fraasi Osborn 1909

When describing this species, based on one mandible, Osborn (1909) figured a maxilla as possibly conspecific and stated that M^3 was absent. That this was probably true in life is indicated by an apparently unbroken vertical surface of bone just posterior to M^2. The presence of an M^3 in *M. fraasi* is, however, proved by a strong shear facet on the postvallid (the posterior wall of the trigonid) of M_3. Furthermore, the postvallid wear is markedly stronger than the prevallid wear in *M. fraasi*, while the reverse is true of the maxilla. Therefore the maxilla is not conspecific with the mandible; the maxilla belongs to a small species of '*Hyaenodon*' as this genus is now defined, despite the presence of a nubbin on M^1 in the place of a protocone.

Propterodon morrisi (Matthew and Granger)

Paracynohyaenodon morrisi Matthew and Granger 1924, p. 1.
Propterodon irdinensis Matthew and Granger 1925, p. 4.

It is clear that the two species of proviverrines described by Matthew and Granger from the Irdin Manha Formation of Mongolia are conspecific. In the type description of *P. morrisi* the two preserved molariform teeth were identified as M_1 and M_3, the latter incompletely erupted. Comparison with the specimens referred to *P. irdinensis* shows, however, that the 'M_3' of *P. morrisi* would be a perfect M_2 in size and morphology for *P. irdinensis* (M_1 and M_3 are known in specimens referred to the latter species) and that the morphology of the mandible is comparable; in particular the posterior mental foramen is under P_3 in both species when the present tooth identifications are used. There is space in the type specimen of *P. morrisi* for an unerupted M_3, and the tooth here identified as DP_4 is low-crowned and narrow and has divergent roots and an anteriorly placed paraconid, all features that are characteristic of the DP_4s of most primitive placentals.

TABLE 1. Measurements of upper teeth, in millimetres. With three or more specimens the standard deviation of the sample (not of the mean) is given, and the number of specimens is in parentheses.

	Anterior margin	Posterior margin	Labial margin*	Mid-width	Posterior height metacone	Labial height paracone
Prototomus torvidus						
P³	—	—	5·5	2·1	—	—
P⁴	4·4, 4·3	6·0, 5·2	5·6, 5·6	4·5, 4·0	—	4·2
M¹	4·6, 4·8	6·7, 6·6	5·5, 5·4	—	4·6	—
M²	5·9±0·2 (3)	8·1, 6·9	5·4, 5·2	—	4·1, 4·4	—
M³	5·4	3·2	2·4, 2·0	—	1·7	—
Proviverra typica						
P⁴	3·8±0·3 (3)	4·3±0·1 (3)	4·5±0·4 (4)	3·3±0·2 (6)	—	3·4±0·3 (3)
M¹	4·8±0·4 (6)	6·3±0·6 (7)	4·6±0·2 (6)	—	3·7, 3·0	—
M²	5·7, 5·9	7·6, 6·8	5·2, 4·5	—	3·6	—
M³	5·9±0·6 (3)	4·1, 3·8	2·4, 2·4	—	—	—
Proviverra minor						
M¹	4·6	5·9	4·3	—	—	—
M²	5·4	6·8	4·5	—	3·2	—
M³	6·1†	—	—	—	—	—
Cynohyaenodon trux						
M¹	5·9	8·6	6·3	—	5·1	—
M²	6·8	8·9, 8·9	5·8	—	4·1, 5·1	—
Cynohyaenodon ruetimeyeri						
P⁴	5·7	7·4, 7·3	6·8	5·6, 5·6	—	—
M¹	6·0±0·1 (4)	9·1, 9·7	6·9, 7·7	—	—	—
M²	6·5, 7·5	10·1, 10·1	6·4, 7·4	—	5·7	—
M³	7·8	4·9	3·0	—	—	—
Prodissopsalis phonax						
P²	—	—	7·2	2·5	—	—
P³	—	—	6·6, 6·7	3·8, 3·4	—	—
P⁴	6·1	8·7	7·2, 8·1	6·1	—	—
M¹	6·9±0·2 (3)	10·1, 10·9	7·8±0·1 (3)	—	5·7	—
M²	8·7, 8·3	12·0, 11·6	7·4±0·2 (3)	—	—	—
M³	8·8, 8·4	5·7, 6·0	3·0±0·2 (3)	—	2·6	—
Prodissopsalis theriodis						
P²	—	—	8·0	8·7	—	—
P³	—	—	4·2	5·8	—	—
P⁴	8·5	11·5	11·3	8·5	—	—
M¹	9·6, 8·7	13·0, 12·1	10·8, 9·7	—	—	—
M²	11·2, 9·7	16·4	14·1	—	—	—

* for M³, length at metacone.   † approximate 95 per cent. confidence interval: ±0·4.

TABLE 2. Measurements of lower teeth, in millimetres.

	Lingual length	Trigonid width	Talonid width	Mandible depth below M_2 protoconid
Prototomus torvidus				7·2*
M_2	4·9†, 5·3	3·5	3·1	
M_3	5·0†, 5·8	3·7	2·8	
Proviverra typica				6·2
P_4	3·6	1·7	—	
M_1	4·3, 4·2	2·3, 2·6	2·3, 2·1	
M_2	4·5, 4·5	2·8, 2·9	2·5, 2·3	
M_3	4·5, 4·7	2·8, 2·7	2·2, 1·9	
Proviverra minor				8·4
P_4	4·6	2·4	—	
M_1	4·7	3·0	2·8	
M_2	5·0	3·4	2·9	
M_3	5·0	3·2	2·2	
Paracynohyaenodon schlosseri				12·5
M_1	7·4	4·3	4·0	
M_2	8·4	4·9	4·2	
M_3	9·0	5·2	3·4	
Cynohyaenodon trux				10·6
P_2	5·4	2·1	—	
P_3	5·4	2·4	—	
P_4	5·8	2·6	—	
M_1	5·7	3·2	2·7	
M_2	6·1	3·7	2·8	
M_3	6·5	3·6	2·2	
Cynohyaenodon ruetimeyeri				14·4, 11·5
P_3	6·2, 5·5	3·2, 2·3	—	
P_4	7·2	3·6	—	
M_1	6·3, 6·3	3·5, 3·4	2·9	
M_2	7·2, 7·0	4·2, 4·2	3·6, 2·8	
M_3	7·0	3·8	2·4	
Prodissopsalis phonax				14·5
M_1	7·1	3·8	3·6	
M_2	8·1	4·4	3·7	
M_3	8·8	4·6	3·6	
Prodissopsalis theriodis				—
P_2	8·3	4·1	—	
P_3	7·8	4·1	—	
P_4	9·4	4·8	—	
M_1	8·8	4·9	4·8	
M_2	9·6, 9·7	5·3, 5·6	5·1, 5·5	
M_3	11·4, 10·7	6·4, 5·7	3·8, 3·3	

* Approximate 95 per cent. confidence interval: ±0·4.   † From Egerkingen β.

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